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2019-05

Malysheva , V , Spirin , V , Miettinen , O , Kout , J , Savchenko , A & Larsson , K-H 2019 , ' On Craterocolla and Ditangium (Sebacinales, Basidiomycota) ' , Mycological Progress , vol. 18 , no. 5 , pp. 753-762 . https://doi.org/10.1007/s11557-019-01485-3

http://hdl.handle.net/10138/301381
https://doi.org/10.1007/s11557-019-01485-3

Mycological Progress (2019) 18:753–762
https://doi.org/10.1007/s11557-019-01485-3

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ORIGINAL ARTICLE

On *Craterocolla* and *Ditangium* (Sebacinales, Basidiomycota)

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Received: 2 October 2018 / Revised: 2 March 2019 / Accepted: 8 March 2019

Abstract
In the present paper, we select a neotype for *Tremella cerasi* and prove that it is conspecific with *Ditangium insigne* (the genus type of *Ditangium*). We argue that *Ditangium* should be restored as a correct genus for *T. cerasi*, while the currently used generic name *Craterocolla* is to be treated as its younger synonym. Morphological, ecological and genetic variability of *Ditangium cerasi* is discussed, and two other *Ditangium* species are described—*D. altaicum*, sp. nov. and *D. incarnatum*, comb. nov. In addition, *Exidia fulva* is combined in *Globulisebacina*.

Keywords Dimorphic fungi · Heterobasidiomycetes · New taxa · Phylogeny · Taxonomy

Introduction

Craterocolla cerasi (Schumach.) Bref. is a jelly fungus well known to mycologists due to a peculiar crater–like anamorphic stage (Hansen and Knudsen 1997; Oberwinkler et al. 2014). According to recent DNA–based studies, *Craterocolla* has been placed to the *Sebacinales* (Agaricomycetes, Basidiomycota) (Weiss et al. 2004; Oberwinkler et al. 2014). In these studies, the genus was considered monotypic i.e., limited to the type species, *Tremella cerasi* Schumach., but no attempts to clarify its identity, as well as the genus concept, were performed.

No type material for *T. cerasi* has been located and its protologue (Schumacher 1803) is obscure and thus opened to controversial interpretations (Donk 1966). In particular, Fries (1822) did not accept this species and simply treated it among synonyms of *Tremella sarcoides* (Jacq.) Fr. (now *Ascocoryne sarcoides* (Jacq.) J.W. Groves & D.E. Wilson, Ascomycota). The current understanding of *T. cerasi* originates from Tulasne and Tulasne (1873). The latter authors associated Schumacher's species name with a jelly fungus inhabiting cherry trees in France and having longitudinally septate, four-celled basidia and cylindrical, curved basidiospores, as well as a characteristic anamorph. When Brefeld (1888) introduced the genus *Craterocolla*, he relied on the Tulasne's understanding of *T. cerasi*, and this interpretation has been accepted by most subsequent authors (Saccardo 1888; Neuhoff 1935, 1936; Pilát 1957 etc.). Two earlier generic names, *Ditangium* P. Karst. (Karsten 1867) and *Poroidea* Göttinger (in Sauter 1880), were treated as heterotypic synonyms of *Craterocolla* (Donk 1966; Wojewoda 1981) but disregarded in favour of the latter.

In the present study, we designate a neotype for *Tremella cerasi* and revise available specimens of *Craterocolla cerasi* from boreal–temperate Northern Hemisphere. The identity of *Ditangium insigne* P. Karst. and *Exidia testacea* Raitv. is clarified based on morphology and DNA studies of types. In addition, a new combination in *Globulisebacina* is proposed. This paper is our homage to Prof. Franz Oberwinkler, one of the most distinguished researchers of jelly fungi, in particular the *Sebacinales*.

This article is part of the "Topic collection on *Basidiomycote Mycology* in honour of Franz Oberwinkler who passed away in March 2018".

Section Editor: Meike Piepenbring

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Material and methods

Type specimens and other collections from herbaria H, LE, O, UPS, TRH, S, TAAM, CWU, as well as from the Mycological Herbarium of the Department of Biology, University of West Bohemia, Czech Republic (informally abbreaviated KBI), were studied. Herbarium acronyms are given according to Thiers (2016). Microscopic routine follows Miettinen et al. (2018). All observations and measurements were made from microscopic slides prepared in Cotton Blue, using phase contrast and oil immersion lens (Leitz Diaplan microscope, × 1250 amplification). At least 20–30 basidiospores and 10–20 conidia were measured for each studied specimen. The following abbreviations are used in microscopic descriptions: *L*–mean cell length, *W*–mean cell width, *Q*′–length/width ratio, *Q*–mean length/width ratio, *n*–number of measurements per specimens measured.

DNA extraction and sequencing For DNA extraction, small fragments of dried basidiocarps were used. In total, 14 specimens were selected for molecular sampling (Table 1). DNA was extracted using the NucleoSpin Plant II Kit (Macherey-Nagel GmbH & Co. KG) according to the manufacturer's instructions. The following primers were used for both amplification and sequencing: ITS1F-ITS4 (White et al. 1990; Gardes and Bruns 1993) for ITS region; primers EF1-983F and EF1-1567R for approximately 500 bp of *tef1* (Rehner and Buckley 2005). PCR products were purified applying the GeneJET Gel Extraction Kit (Thermo Scientific, Thermo Fisher Scientific Inc., MA, USA). Sequencing was performed with an ABI model 3130 Genetic Analyzer (Applied Biosystems, CA, USA). Raw data were edited and assembled in MEGA 6 (Tamura et al. 2013).

Phylogenetic analyses For this study, 19 ITS and 15 *tef1* sequences were generated. Additionally, four sequences (three nrITS and one *tef1*) including the outgroups were retrieved from GenBank (www.ncbi.nlm.nih.gov/genbank/). GenBank matches as well as preliminary multiple alignments prepared by us showed that *tef1* sequences of *Ditangium* spp. obtained for this study contain two introns. These introns were

Table 1 Data for nrITS and tef1 sequences used in the phylogenetic analyses

Species	Collector/herbarium number	Origin (ISO code)	Host	nrITS GenBank #	tef1 GenBank #	Source
Ditangium altaicum	LE 231836	RU	Alnus sp.	MH836338	MH910034	This study
D. cerasi	2.I.2010 Kout (KBI, H) X4196	CZ	Cerasus sp.	MH836373	–	This study
D. cerasi	30.IX.2002 Kout (KBI, H) X4197	CZ	Cerasus sp.	MH836374	MH910035	This study
D. cerasi	Karsten 3508 (H)	FI	Picea abies	MH836341	–	This study
D. cerasi	Hyvärinen (H ex O)	FI	Betula sp.	MH836326	–	This study
D. cerasi	Junninen 2314 (H)	FI	Picea abies	MH836327	MH910021	This study
D. cerasi	VS 11073 (O)	NO	Alnus incana	MH836329	–	This study
D. cerasi	LE 254072	RU	Picea orientalis	MH836335	MH910028	This study
D. cerasi	LE 254074	RU	Picea orientalis	MH836340	MH910030	This study
D. cerasi						This study
D. cerasi	LE 254073	RU	Abies nordmanniana	MH836339	MH910029	This study
D. cerasi	LE 312775	RU	Pinus sibirica	MH836334	MH910027	This study
D. cerasi	TAAM 9173	RU	Abies sibirica	MH836342		This study
D. cerasi	VS 3846 (H)	RU	Picea ajanensis	MH836330	MH910024	This study
D. cerasi	VS 3889 (H)	RU	Pinus pumila	MH836332	MH910026	This study
D. cerasi	VS 4677 (H)	RU	Picea abies	MH836328	MH910022	This study
D. cerasi	VS 10466 (H)	RU	Betula pubescens	MH836331	MH910025	This study
D. cerasi	LE 294521	RU	Pinus koraiensis	MH836333	MH910023	This study
Craterocolla cerasi	AFTOL-ID 1677	–	–	DQ520103	–	Unpublished
C. cerasi	strain TUB 020202	DE	fruit body on stems of Prunus avium	KF061264	–	Oberwinkler et al. 2014
D. incarnatum	Haikonen 28,811 (H)	FI	Populus tremula	–	MH910031	This study
D. incarnatum	LE 206311	RU	Populus tremula	MH836336	MH910033	This study
D. incarnatum	LE 303419	RU	Populus tremula	MH836337	MH910032	This study
Serendipita vermifera	strain MAFF305835	AU	Orchid mycorrhiza of Caladenia catenata	DQ983814	JN211116	Deshmukh et al. 2006

phylogenetically informative, and therefore they were not removed from the phylogenetic analyses.

Sequences were aligned with the MAFFT version 7 web tool (http://mafft.cbrc.jp/alignment/server/) using the Q-INS-i option for nrITS. Phylogenetic reconstructions for three data sets (nrITS, *tef1*, nrITS+*tef1*) were performed with maximum likelihood (ML) and Bayesian (BA) analyses. Before the analyses, the best-fit substitution models for the alignment were estimated for each dataset based on Akaike Information Criterion (AIC) using FindModel web server (http://www.hiv.lanl.gov/content/sequence/findmodel/findmodel.html). Selected models were as follows: 'GTR plus Gamma' for nrITS dataset; 'GTR' for nrITS+*tef1* dataset; 'TrN: Tamura-Nei plus Gamma' for *tef1* dataset.

ML analyses were run in the PhyML server, v. 3.0 (http://www.atgc-montpellier.fr/phyml/), with 1000 rapid bootstrap replicates. BA was performed with MrBayes 3.2.5 software (Ronquist et al. 2012), under selected model for each data set, for two independent runs, each with 5 million generations with sampling every 100 generations and four chains. Tracer v. 1.6.0 (Rambaut et al. 2014) was used to evaluate the quality of a sample from the posterior and the continuous parameters, using effective sample size (ESS). We accepted the result where the ESS (effective sample size) was above 200 and the PSRF (potential scale reduction factor) was close to 1. The clades with posterior probability (PP) value > 0.95 were considered to be significantly supported.

Newly generated sequences have been submitted to GenBank (Table 1) and alignments to TreeBase (S23714, S23715, S23721).

Specimens examined (sequenced specimens are marked by asterisk)

Ditangium altaicum. Russia. Altai Republic: Ulagan Dist., Altai Nat. Res., *Alnus* sp., 18.VIII.2008 *Malysheva* (LE 231836*, holotype).

D. cerasi. Czech Republic. Central Bohemia: Roztoky, Řivnáč hill, *Prunus cerasus*, 2.I.2010 *Kout** (KBI, H 7008918). South Bohemia: Tábor, Chýnov, *P. cerasus*, 30.IX.2002 *Kout* (H 7008919*–neotype of *Tremella cerasi*, KBI–isoneotype). Finland. Etelä-Häme: Tammela, Mustiala, *Picea abies*, 10.X.1866 *Karsten 3508** (H, lectotype of *Ditangium insigne*). Perä-Pohjanmaa: Tervola, Hirvikumpu, *Betula* sp., 20.X.2005 *Hyvärinen** (H). Kittilän Lappi: Kolari, Kesänkijärvi, *P. abies*, 6.V.2016 *Junninen 2314** (H). France. Aveyron: St. Sernin, *P. cerasus*, III.1905 *Galzin 810* (herb. Bourdot 4566) (UPS). Germany. Bayern: Garmisch-Partenkirchen, Oberammergau, *P. abies*, VIII.1894 *Schnabl* (as *Poroidea pithyophila*, H ex Fungi Bavarici #936). Norway. Vest-Agder: Mandal, Uføra, *Quercus robur*, 2.XI.2017 *Spirin 11773* (O). Oppland: Sel, Sagåa Nat. Res., *Alnus incana*, 13.IX.2016 *Spirin 11073** (O). Nor-Trøndelag: Steinkjer, Byahalla Nat. Res., *A. incana*, 11.V.2014 *Holien 22/14* (TRH F15861). Russia. Karachaevo-Cherkessia: Karachaevsk Dist, Teberda Nat. Res., *Picea orientalis*, 8.VIII.2009 *Malysheva* (LE 254072*, LE 254074*), *Abies nordmanniana*, 12.VIII.2009 *Malysheva* (LE 254073*). Komi Rep.: Troitsko-Pechersky Dist., Pechoro-Ilych Nat. Res., *P. abies*, 13–15.IX.1992 *Hermansson & Lundqvist* (UPS F-013743, F-013748), *Pinus sylvestris*, 19.IX.1992 *Hermansson & Lundqvist* (UPS F-141037). Krasnoyarsk Reg.: Ermakovskoe Dist., Sayano-Shushensky Nat. Res., *Pinus sibirica*, 27.VIII.2015 *Malysheva* (LE 312775*); Mansky Dist., Badzhei, *Abies sibirica*, 6.IX.1958 *Parmasto* (TAAM 9173*, holotype of *Exidia testacea*). Khabarovsk Reg.: Solnechny Dist., Igdomi, *Picea ajanensis*, 6.VIII.2011 *Spirin 3846** (H), *Pinus pumila*, 6.VIII.2011 *Spirin 3889** (H). Leningrad Reg.: Boksitogorsk Dist., Kolp', *P. abies*, 26.IX.2011 *Spirin 4677** (H), Vozhani, *Betula pubescens*, 30.VII.2016 *Spirin 10466** (H). Primorie. Ternei Dist.: Sikhote-Alin Nat. Res., *Pinus koraiensis*, 24.VIII.2012 *Malysheva* (LE 294521*). Slovakia. Banská Bystrica: Banská Štiavnica, Prenčov, *Malus* sp., 3.XI.1896 *Kmet* (UPS). Ukraine. Ivano-Frankivsk Reg.: Nadrivna Dist., Carpathian Nat. Park, *P. abies*, VI.2011 *Akulov* (CWU 7018).

D. incarnatum. Finland. Etelä-Häme: Iitti, Säyhtee, *Populus tremula*, 25.IV.2012 *Haikonen 28811** (H); Tammela, Mustiala, *Salix pentandra*, 1.IX.1886 *Karsten 1324* (H 6049583, lectotype of *Dacrymyces incarnatus*). Norway. Akershus: Nannestad, Sundby, *P. tremula*, 17.IX.1964 *Eckblad* (O F160849). Russia. Leningrad Reg.: Priozersk Dist., Otradnoe, *P. tremula*, 7.X.1995 *Zmitrovich* (LE 206311*). Primorie. Ternei Dist.: Sikhote-Alin Nat. Res., *P. tremula*, 20.VIII.2012 *Malysheva* (LE 303419*).

Globulisebacina fulva. Portugal. Castelo Branco: São Fiel, *Eucalyptus globulus*, XII.1903 *Torrend 438* (S F20578, lectotype of *Exidia fulva*).

Results

While discussing generic names of the European heterobasidiomycetes, Donk (1966) preferred *Craterocolla* as the correct genus for *T. cerasi* and rejected two older genera, *Ditangium* and *Poroidea*, since they were based on anamorphic stages. His solution followed Art. 59 of the Montreal Code (1961) and was accepted by the subsequent authors. However, Art. F.8.1 of the current Code (2018) prescribes to choose the oldest legitimate name, whether teleomorphic or anamorphic, for naming a genus. Therefore, *Ditangium* should be used instead of *Craterocolla* if we assume that their type species, *D. insigne* P. Karst. and *T. cerasi*, are congeneric.

The protologue of *T. cerasi* (Schumacher 1803: 438) gives no clear answer what was the species it had been intended for. It referred to a jelly fungus with cerebriform, substipitate, reddish fructifications ('gyroso-lobata substipitata dilute purpurascens diaphana') occurring on bark and wood of cherry trees in Denmark. Donk (1966) argued that it most probably implies the

imperfect stage of an ascomycete; he was apt to associate it with *Sirobasidium cerasi* Bourdot & Galzin. If his opinion is accepted, then *T. cerasi* becomes an older name for *S. cerasi* and *Craterocolla* replaces *Endostilbum* Malençon (Ascomycota) at the generic level. We find these taxonomic changes disadvantageous and prefer to follow the prevailing understanding of *T. cerasi* as a heterobasidiomycete with a characteristic anamorphic stage (see also Recommendation 9A4 of the Code). To confirm this tradition, a neotype for *T. cerasi* is designated below.

Neuhoff (1935) considered *T. cerasi* (as *Ditangium cerasi* (Schumach.) Costantin & L.M. Dufour) and *D. insigne* (the generic type of *Ditangium*) as taxonomic synonyms. On the other hand, Laurila (1939) and Eriksson (1958) continued to label North European collections as *D. insigne*. They argued that different distribution areas (temperate versus boreal Europe) and host preferences (*Prunus cerasus* versus *Picea*) supported the interpretation that two independent 'biological species' were present. In order to investigate this hypothesis, the authentic specimen of *D. insigne* (selected as a lectotype below), the holotype of *Exidia testacea* Raitv. (synonymized with *C. cerasi* by Malysheva 2012) and 19 specimens of *D. cerasi* s.l. collected from various host over temperate–boreal Eurasia have been studied by morphological and DNA methods.

Analyses of three datasets and their comparison with morphological (macroscopic and microscopic features of basidiocarps) and ecological (host preferences) features, as well as geographic patterns, give us the following results:

1. nrITS phylogeny. The final alignment contained 584 characters (including gaps). The overall topologies of the ML and BI trees were visually identical and divided ITS sequences in two groups (Fig. 1):

    1) a large group (pp = 0.92, bs = 74) containing sequences from lectotype of *D. insigne*, holotype of *E. testacea* and 16 other specimens of which 14 are obtained for the present study. ITS sequences of two specimens found on *P. cerasus* in Czech Republic (X4196, 4197), one Norwegian specimen from *Alnus incana* (VS 11073) and two Caucasian collections from coniferous hosts (LE 254073, 254074) are identical while the rest of sequences (specimens from coniferous hosts and *Betula* spp., all but one from boreal or continental parts of Eurasia) show small differences (3–6 bp) from them. As said above, *T. cerasi* was described from temperate Europe (Denmark) as inhabiting bark and wood of *P. cerasus*. Consequently, we select one of the sequenced specimens found on cherry tree in temperate Europe (Czech Republic) as a neotype of *T. cerasi* (see below);
    2) a small clade (pp = 0.99, bs = 86) containing sequences of two specimens found on *Populus tremula* (LE 206311 from North-West Russia and LE 303419 from Russian Far East) plus one collection from *Alnus* (LE 231836, Altai). Four bp difference exists between aspen- and alder-dwelling specimens. The variability of the ITS region in both clades prompted us to produce a *tef1* dataset.

2. *tef1* phylogeny. The final alignment contained 612 characters (including gaps). All clades detected in *tef1* phylogeny are strongly supported and the overall picture is more nuanced (Fig. 2).

    1) a large clade with *T. cerasi* neotype (pp = 0.96, bs = 87) is divided in three lineages:

- lineage A includes the neotype of *T. cerasi* and three collections from Caucasus; conidial stage is usually present and develops separately from the teleomorph, conidia are slightly or distinctly curved;
- lineage B includes two specimens from North Europe morphologically identical to the type of *D. insigne*; conidia are of the same shape as in the previous clade, slightly or distinctly curved but on average longer;
- lineage C includes five collections from the continental parts of Eurasia; conidial stage is rare and it develops directly on teleomorphic fructifications, conidia moderately or strongly curved and on average wider than in the two previous subclades;

    2) a small clade (pp = 1, bs = 100) containing specimens from *Alnus* and *Populus* which have no crater-like anamorphic stage. This clade is represented by two lineages interpreted here as two different species:

- three aspen-dwelling specimens (LE 206311, LE 303419 plus VH 28811 from Finland) having identical *tef1* sequences are named *Ditangium incarnatum* (based on *Dacrymyces incarnatus* P. Karst., see below);
- the *Alnus*-dwelling specimen LE 231836 showing considerable difference (4%) in *tef1* region versus *D. incarnatum* represents a new species, *D. altaicum*.

3. Combined nrITS + *tef1* phylogeny. The final alignment contained 1219 characters (including gaps). The two-gene combination was not effective enough to clarify the relationships within the group further. However, nrITS + *tef1* phylogeny clearly uncovers three lineages corresponding to the three morphological species—*D. altaicum*, *D. incarnatum* and *D. cerasi* (Fig. 3). The combined phylogeny does not support further splitting of the latter lineage, as opposed to morphological data and, partly, geographic distribution and host preferences. This problem should be addressed by using still other genetic markers. For the moment, we accept Neuhoff's opinion and treat *T. cerasi* and *D. insigne* as taxonomic synonyms.

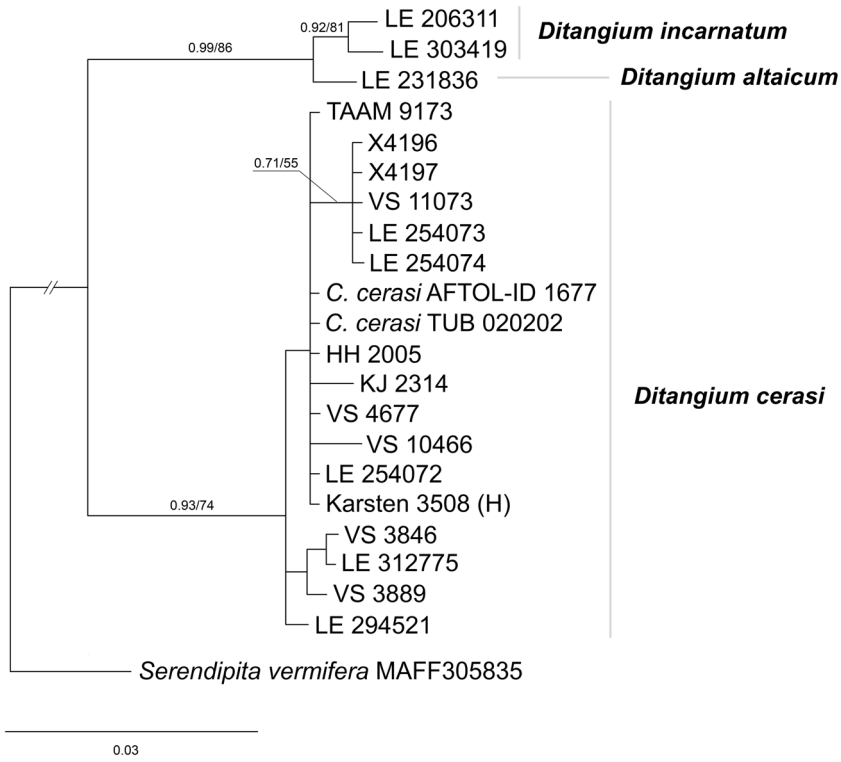

Fig. 1 Bayesian phylogram for the nrITS dataset. Collection numbers are given for all sequences. Support values (Bayesian posterior probability/maximum likelihood bootstrap values) are given above the branches. Scale bar shows expected changes per site

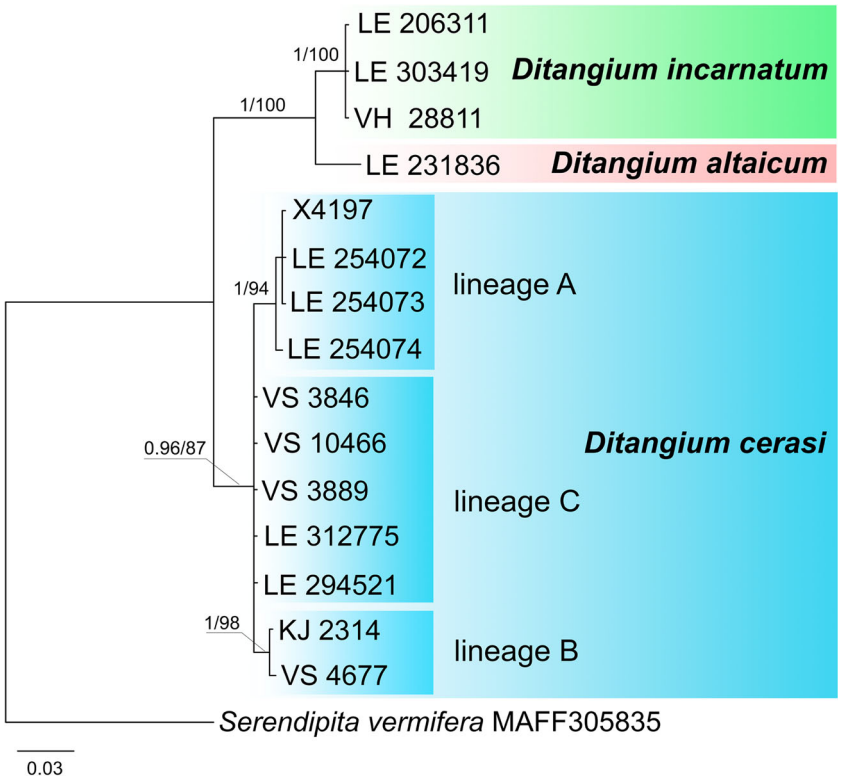

Fig. 2 Bayesian phylogram for the *tef1* dataset showing major lineages of *Ditangium*. Collection numbers are given for all sequences. Support values (Bayesian posterior probability/maximum likelihood bootstrap values) are given above the branches. Scale bar shows expected changes per site

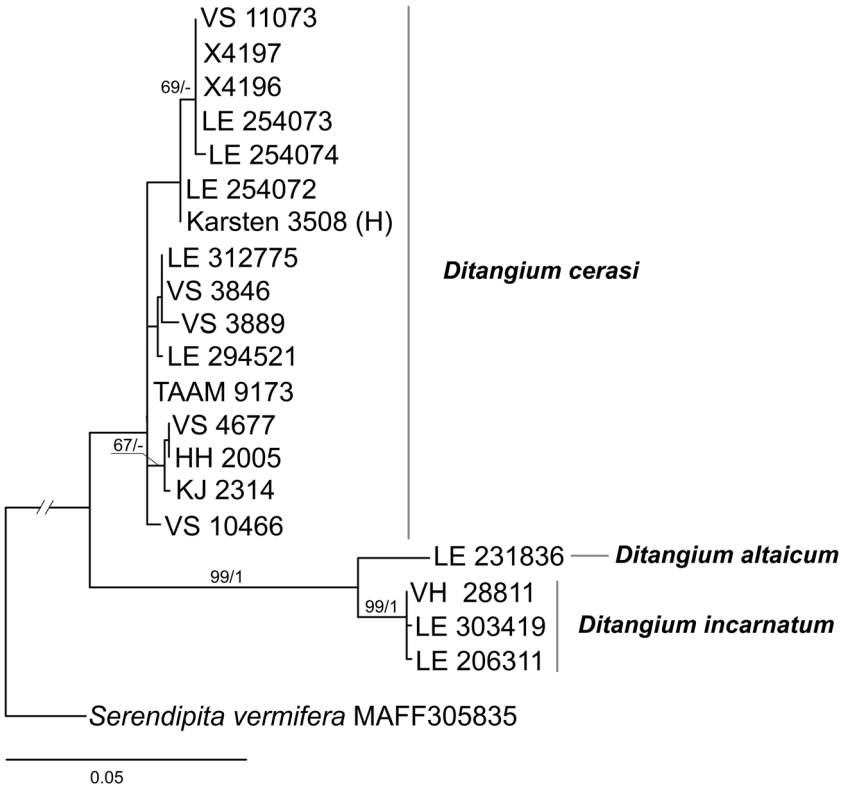

Fig. 3 Combined nrITS + *tef1* topology from ML analysis. Collection numbers are given for all sequences. Support values (maximum likelihood bootstrap values/Bayesian posterior probability) are given above the branches. Scale bar shows expected changes per site

Taxonomy

Ditangium P. Karst., Notiser Sällsk. Fauna Flora Fennica Förhandl. 11: 213, 1870.

Basidiocarps pustulate or cerebriform, small- to medium-sized, pink to brick-red. Conidial fructifications occasionally present, appearing on or together with teleomorphic basidiocarps, crater-like. Monomitic; hyphae clampless, abundantly encrusted by oily matter. Hyphidia abundant, covering hymenial surface, sparsely or richly branched. Basidia (2) 4-celled, obovate to subglobose, longitudinally or obliquely septate. Basidiospores hyaline, thin-walled, narrowly fusiform to cylindrical. Hyphae of anamorphic fructifications similar to those of the teleomorph; conidia thin-walled, cylindrical, slightly to strongly curved. On wood of deciduous trees and conifers at an early stage of decompostition.

Genus type. *Ditangium insigne* P. Karst.

The genus is re-introduced here to encompass three closely related species (see below). No material from North and South America has been available for this study. The identity of two species currently associated with *Ditangium* i.e., *Dacrymyces conglobatus* Peck from the north-eastern part of the USA and *Ditangium minutum* Pat. from Ecuador, should be re-checked based on newly collected material from those areas.

Ditangium altaicum V. Malysheva & Spirin, sp. nov. (Fig. 4a).

Holotype. Russia. Altai Republic: Ulagan Dist., Altai Nat. Res., *Alnus* sp., 18.VIII.2008 *Malysheva* (LE 231836).

MB 827990

Basidiocarps cerebriform, 3–7 mm in diam. and 1.5–3 mm thick, pink to brick-red. Conidial fructifications absent. Hyphae clampless, interwoven or ascending, abundantly encrusted by oily matter; tramal hyphae thin-walled, 1.5–2.5 μm in diam., subhymenial hyphae thin-walled, 1–2.5 μm in diam. Hyphidia abundant, covering hymenial surface, richly branched, apical branches 1–1.2 μm in diam. Basidia (2) 4-celled, obovate to subglobose, (8.0–) 8.1–9.9 (− 11.0) × (6.7–) 6.8–7.8 (− 8.0) μm ($n = 20/1$), sterigmata up to 22 × 1–1.5 μm. Basidiospores narrowly fusiform, straight or slightly concave, (7.8–) 8.0–10.3 (− 11.8) × (2.8–) 2.9–3.3 (− 3.6) μm ($n = 30/1$), $L = 9.11$, $W = 3.11$, $Q' = (2.3–) 2.6–3.4 (− 3.6)$, $Q = 2.93$.

Remarks: *Ditangium altaicum* possesses small-sized basidiocarps and no conidial stage and thus it is more or less macroscopically identical to *D. incarnatum*. These species can be separated mainly due to differently looking basidiospores–fusiform and almost always straight in *D. altaicum* and cylindrical and often clearly curved in *D. incarnatum*. *Ditangium altaicum* is so far known only from the locus classicus in Siberia.

Ditangium cerasi (Schumach.) Costantin & L.M. Dufour, Nouvelle flore des champignons: 207, 1891. (Figs. 4b, 5 and 6a–c).

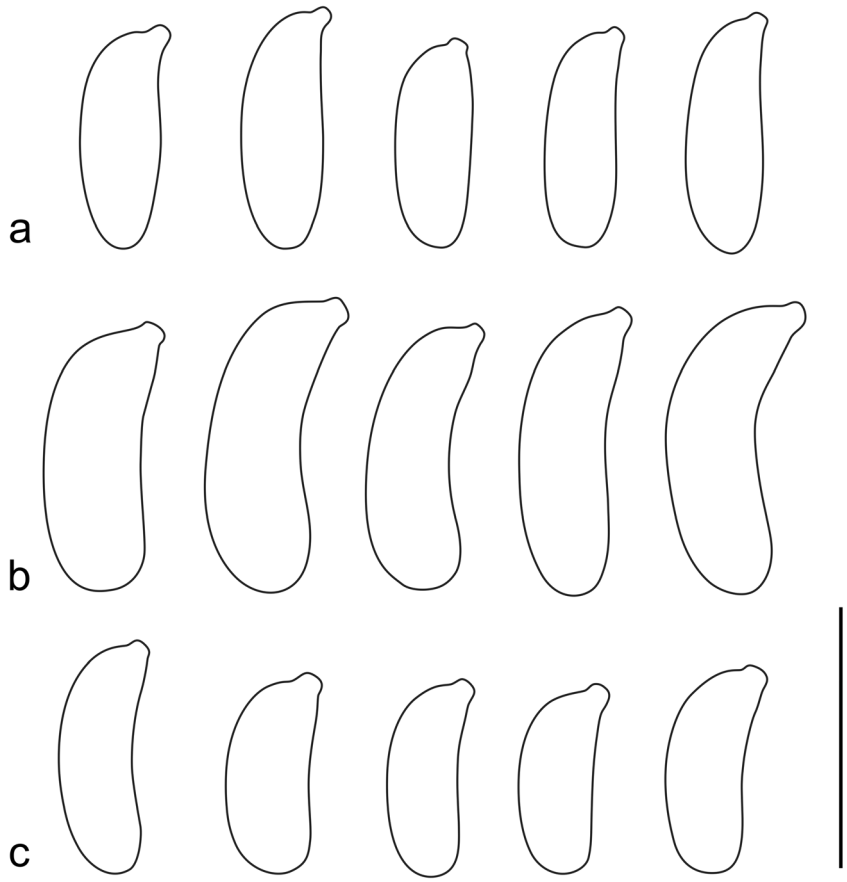

Fig. 4 Basidiospores of *Ditangium* spp.: **a** *D. altaicum* (LE 231836, holotype), **b** *D. cerasi* (VS 10466), **c** *D. incarnatum* (LE 206311). Scale bar—10 μm

≡ *Tremella cerasi* Schumach., Enumeratio Plantarum, in Partibus Saellandiae Septentrionalis et Orientalis Crescentium 2: 438, 1803. Neotype (selected here). Czech Republic. South Bohemia: Tábor, Chýnov, *Prunus cerasus*, 30.IX.2002 *Kout* (H 7008919, isoneotype–KBI) (MBT 383584).

≡ *Craterocolla cerasi* (Schumach.) Bref., Unters. Gesamtgeb. Mykol. 7: 99, 1888.

≡ *Exidia cerasi* (Schumach.) Ricken, Vadem. Pilzfr.: 274, 1918.

= *Ditangium insigne* P. Karst., Fungi Fenniae Exsiccati 7: 656, 1867. Lectotype (selected here). Finland. Etelä-Häme: Tammela, Mustiala, *Picea abies*, 10.X.1866 *Karsten 3508* (H) (MBT 383585).

= *Poroidea pithyophila* Göttinger in Sauter (as *pityophila*), Mitt.Gesellsch. Salzburger Land. 20: 218, 1880 (fide Donk 1966).

= *Exidia testacea* Raitv., Plants and Animals of the Far East: 117, 1971. Holotype. Russia. Krasnoyarsk Reg.:

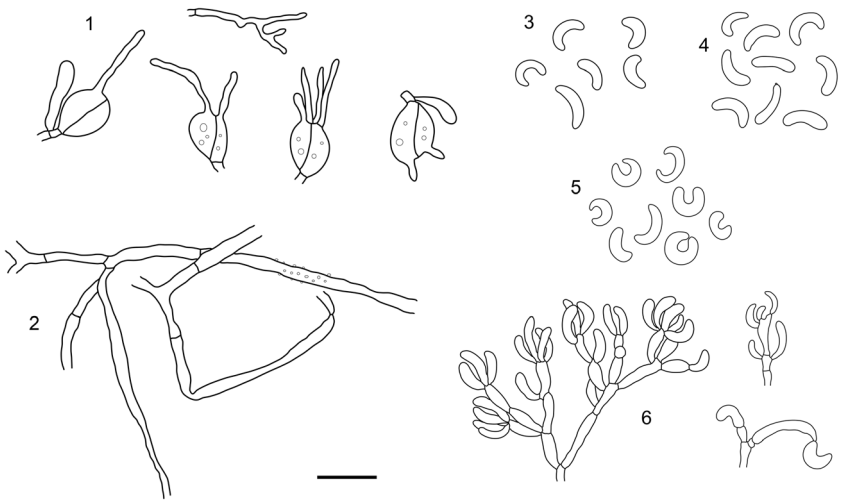

Fig. 5 Microstructures of *Ditangium* spp.: (1) *Ditangium cerasi* (VS 10466): basidia and hyphidia; (2) *D. cerasi* (VS 10466): subhymenial hyphae; (3) conidia of *D. cerasi* (lineage A) (LE 254072); (4) conidia of *D. cerasi* (lineage B) (Karsten 3508); (5) conidia of *D. cerasi* (lineage C) (VS 3889); (6) conidiophores of *D. cerasi* (LE 254072—left, VS 3889—right). Scale bar—10 μm

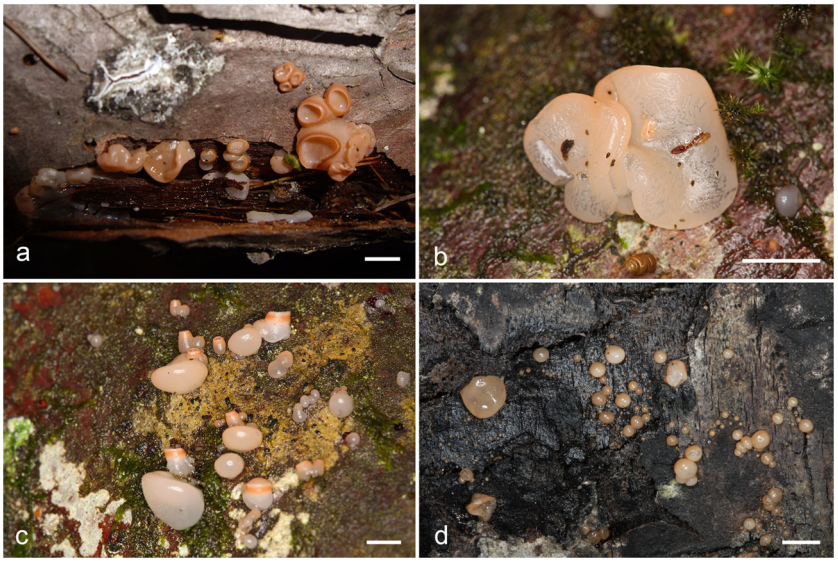

Fig. 6 Fructifications of *Ditangium* spp.: **a** *D. cerasi* (VS 3889, lineage C) (teleomorph and anamorph), **b** *D. cerasi* (LE 254073, lineage A) (old discoloured teleomorph), **c** *D. cerasi* (LE 254074, lineage A) (teleomorph and anamorph), **d** *D. incarnatum* (LE 303419). Scale bar—5 mm

Mansky Dist., Badzhei, *Abies sibirica*, 6.IX.1958 *Parmasto* (TAAM 9173).

Basidiocarps cerebriform, 5–20 mm in diam., 3–8 mm thick, pink to brick-red, senescent basidiocarps sometimes fading to almost white. Conidial fructifications occasionally present, appearing on or together with teleomorphic basidiocarps, crater-like, 1–2 mm in diam. Hyphae clampless, interwoven or ascending, abundantly encrusted by oily matter; tramal hyphae thin- to slightly thick-walled, (1.5–) 2–4 μm in diam., occasionally inflated up to 5 μm in diam., subhymenial hyphae thin-walled, (1–) 1.5–3 μm in diam. Hyphidia abundant, covering hymenial surface, sparsely or richly branched, apical branches 1–2 μm in diam. Basidia (2) 4-celled, obovate to subglobose, (7.8–) 8.1–11.2 (− 12.8) × (6.1–) 6.6–9.6 (− 10.0) μm (n = 65/8), sterigmata up to 30 × 1–2 μm. Basidiospores narrowly cylindrical to cylindrical, slightly to distinctly curved, (7.1–) 7.2–12.9 (− 15.2) × (2.6–) 2.7–4.4 (− 4.5) μm (n = 320/13), L = 8.32–10.72, W = 2.98–3.95, Q' = (2.0–) 2.1–3.9 (− 4.1), Q = 2.44–3.34. Hyphae of anamorphic fructifications similar to those of a teleomorph but often with thickened walls (except thin-walled conidiiferous branches); conidia thin-walled, cylindrical, predominantly slightly to moderately curved (lunate), (4.8–) 4.9–8.2 (− 9.2) × (1.7–) 1.8–2.3 (− 2.6) μm (n = 60/3), L = 5.63–6.91, W = 1.97–2.20, Q = 2.87–3.27 (lineage A–Fig. 5.3) or (5.2–) 5.8–8.8 (− 9.4) × (1.6–) 1.8–2.5 (− 2.8) μm (n = 49/3), L = 7.06–7.67, W = 1.98–2.27, Q = 3.38–3.58 (lineage B–Fig. 5.4), or moderately to strongly curved, (5.7–) 5.8–8.9 (− 9.1) × (2.1–) 2.2–3.0 (− 3.1) μm (n = 20/1), L = 6.88, W = 2.62, Q = 2.66 (lineage C–Fig. 5.5).

Remarks: As understood here, *D. cerasi* is a widespread species in Eurasia although it is rarely collected. It occurs on various hosts—both conifers (*Abies*, *Picea*, *Pinus*) and deciduous trees (*Alnus*, *Betula*, *Malus*, *Prunus*, *Quercus*).

Ditangium incarnatum (P. Karst.) Spirin & V. Malysheva, comb. nov. (Figs. 4c and 6d).

≡ *Dacrymyces incarnatus* P. Karst., Medd. Soc. Fauna Fl. Fennica 14: 83, 1887. Lectotype (selected here). Finland. Etelä-Häme: Tammela, Mustiala, *Salix pentandra*, 1.IX.1886 *Karsten 1324* (H 6049583) (MBT 383580).

MB 827991

Basidiocarps normally pustulate, 1–1.5 mm in widest dimension, rarely fusing together and then cerebriform, up to 5–6 mm in diam. and 3–4 mm thick, pink to yellowish-cream. Conidial fructifications absent. Hyphae clampless, interwoven or ascending, abundantly encrusted by oily matter; tramal hyphae thin- to slightly thick-walled, (2–) 2.5–3.5 μm in diam., subhymenial hyphae thin-walled, 1–2.5 μm in diam. Hyphidia abundant, covering hymenial surface, richly branched, apical branches 0.8–1.2 μm in diam. Basidia (2) 4-celled, obovate to subglobose, (7.1–) 7.2–10.6 (− 11.0) × (6.1–) 6.2–8.0 (− 8.1) μm (n = 30/3), sterigmata up to 34 × 1–1.5 μm. Basidiospores narrowly cylindrical, slightly to distinctly curved, (6.0–) 6.3–10.2 (− 10.3) × (2.6–) 2.7–3.6 (− 3.7) μm (n = 80/4), L = 7.10–8.72, W = 2.94–3.09, Q' = (2.1–) 2.2–3.3 (− 3.5), Q = 2.42–2.87.

Remarks: This species was described by Karsten (1887) based on a single collection from Finland but it has remained unknown or unrecognised (cf. McNabb 1973). Morphological study revealed that Karsten's type is identical to four other specimens collected on wood of *Salicaceae* in temperate–hemiboreal Eurasia. *Ditangium incarnatum* differs from *D. cerasi* in having essentially smaller basidiocarps and on average shorter basidiospores. No conidial stage associated

with *D. incarnatum* has been detected. The closely related *D. altaicum* has differently shaped (fusiform) basidiospores.

Globulisebacina fulva (Bres. & Torrend) Spirin, comb. nov.

≡ *Exidia fulva* Bres. & Torrend, Brotéria, Sér. Bot. 11: 89, 1913. Lectotype (selected here). Portugal. Castelo Branco: São Fiel, *Eucalyptus globulus*, XII.1903 *Torrend 438* (S F20578) (MBT 383582).

MB 827992

Basidiocarps pustulate or cupulate, gregarious, gelatinous, yellowish to brownish, 1–1.5 mm in diam., 0.1–0.3 mm thick, partly fusing but remaining discernable. Hyphal structure monomitic. Hyphae ascending, hyaline to brownish, richly branched, some twisted, simple-septate, (2.0–) 2.2–3.3 (−3.7) μm in diam. ($n = 20/1$), CB (+), some hyphae bearing amorphous brownish incrustation (seen in Cotton Blue). Cystidia absent; hyphidia abundant, covering hymenial surface, hyaline to brownish, richly branched, 1.5–2.5 μm in diam. at the apical part. Basidia broadly ellipsoid to ovoid, hyaline to pale brownish, 2–4-celled, with longitudinally or obliquely oriented inner septa, 11.5–16 × 9–11.5 μm ($n = 12/1$), without a basal clamp, some senecent basidia slightly thick-walled; sterigmata subulate, up to 15 × 2.5–4 μm. Basidiospores cylindrical, more or less clearly curved, hyaline, thin-walled, (11.3–) 12.0–15.8 (− 18.2) × (4.5–) 4.8–7.7 (− 7.8) μm ($n = 20/1$), $L = 14.07$, $W = 6.20$, $Q' = (1.8–)\ 2.0–2.6\ (-2.8)$, $Q = 2.30$.

Remarks: Searching for older names potentially connected to *Ditangium* spp. led us to *Exidia fulva*, a completely forgotten species described from Portugal. Yellowish or brownish basidiocarps and encrusted, clampless hyphae of the lectotype are reminiscent of *Ditangium* although basidia and basidiospores of *E. fulva* are essentially larger. In our opinion, *E. fulva* is very similar to or probably identical with *Exidia rolleyi* L.S. Olive as the latter has been introduced by Olive (1958), Wells (1975) and Roberts (2011). The latter species was placed in *Efibulobasidium* K. Wells (Wells 1975) and recently moved to its own genus, *Globulisebacina* Oberw. et al. (2014) (Sebacinales, Basidiomycota). Therefore, a new combination in *Globulisebacina* is proposed.

Acknowledgments The curators of herbaria TAAM, UPS, CWU, S, TRH are thanked for providing specimens for loan.

Funding information Open access funding provided by University of Helsinki including Helsinki University Central Hospital. The research was supported by Norwegian Biodiversity Information Centre (the project 'A survey of Norwegian jelly fungi', grant number knr. 44-15) (the authors KHL and VS), by Komarov Botanical Institute, Russian Academy of Sciences (project AAAA-A19-119020890079-6) (the author VM), by the Estonian Science Agency (project IUT20-30) and the European Union through the European Regional Development Fund (Centre of Excellence FIBIR) (the author AS).

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